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ADVANCES IN APOCYNACEAE:
THE ENLIGHTENMENT,
AN INTRODUCTION¹

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ABSTRACT

This issue of the *Annals of the Missouri Botanical Garden* is devoted to advances in the Apocynaceae s.l. and is based on the symposium, “Recent Progress in the Systematics of Apocynaceae,” held at the XVII International Botanical Congress in Vienna in 2005. The collection of papers presented here spans the phylogenetic and geographic breadth of the family and includes at least one study focused on representatives from each of the five subfamilies: Rauvolfioideae, Apocynoideae, Periplocoideae, Secamonoideae, and Asclepiadoideae. The papers range from higher-level phylogenetic analyses to more narrowly defined case studies and include new results in phylogenetics, taxonomy, biogeography, pollination biology, and a pharmacophagous plant–butterfly interaction involving pyrrolizidine alkaloids, as well as a new hypothesis for the evolution of pollinia and loss of a compitum in some advanced taxa. An updated classification scheme of the Apocynaceae is presented, with one additional tribe recognized in Rauvolfioideae (the Aspidospermeae) and three in Apocynoideae (the Nerieae and Odontadenieae as well as the Baisseeae, which are elevated in rank here). In Asclepiadoideae, seven subtribes are recognized within Asclepiadeae (the Asclepiadinae, Cynanchinae, Tylophorinae, Metastelmatinae, Orthosiinae, Oxypetalinae, and Gonolobinae) and four within Ceropegieae (the Anisotominae, Leptadeniinae, Heterostemminae, and Stapeliinae). Taken together, the papers here present the most up-to-date overview of the family available at this time.

Key words: Apocynaceae s.l., Apocynoideae, Asclepiadoideae, classification, monophyly, paraphyly, Periplocoideae, pharmacophagy, phylogeny, pollination biology, pollinia, pyrrolizidine alkaloids, Rauvolfioideae, Secamonoideae, systematics.

The issue you hold in your hands is the second Apocynaceae symposium issue and represents papers and posters presented in the symposium, “Recent Progress in the Systematics of Apocynaceae,” held at the XVII International Botanical Congress in Vienna, which took place in July 2005. The 13 papers span the breadth of the Apocynaceae s.l., with contributions on

all subfamilies and including new results in phylogenetic systematics, taxonomy, biogeography, pollination biology, and a pharmacophagous plant–animal mutualism between a species of *Prestonia* R. Br. (Echiteae) containing pyrrolizidine alkaloids and the lepidoptera that utilize them, as well as a new hypothesis for the evolution of pollinia and loss of

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a compitum in some advanced taxa. Phylogenetic methods, especially those based on molecular data, indicate the presence of rampant parallel evolution throughout the family, involving numerous morphological characters, many of which were previously used as key characters in delimiting higher-level taxa (e.g., syncarpy vs. apocarpy, and fruit and seed type in Rauvolfioideae; corona structure in Asclepiadoideae) and some of which were once considered to be such complex characters that it was taken for granted that they could only have arisen once (e.g., pollinia). It is the most up-to-date compilation of papers currently available on Apocynaceae and is testimony to the significant advances since the first symposium volume.

The first symposium volume included seven papers published in volume 88 of the *Annals of the Missouri Botanical Garden* in 2001 and was based on talks presented in the symposium, “Evolution and Phylogenetics of the Apocynaceae s.l.,” at the XVI International Botanical Congress held in St. Louis, Missouri, in 1999. Therein, the backbone of a consensus classification for the family was presented that included five subfamilies and 18 tribes (Endress & Stevens, 2001), and the broad acceptance of the reunification of Apocynaceae and Asclepiadaceae was announced for the first time since they were sundered by Robert Brown in 1810. Thus its title: *The Renaissance of the Apocynaceae s.l.: Recent Advances in Systematics, Phylogeny, and Evolution*.

In the six years since the publication of the first Apocynaceae symposium volume, Apocynaceae systematics has seen unabated activity, particularly within the largest subfamily, Asclepiadoideae. A number of phylogenetic studies focused on Asclepiadoideae, the largest tribe of Asclepiadoideae, have brought a wealth of new information, allowing a much better understanding of the intertribal relationships. Two major clades have now emerged: the predominantly Old World ACT clade (including the Asclepiadinae Endl. ex Meisn., Cynanchinae K. Schum., and Tylophorinae (K. Schum.) Liede) and the exclusively New World MOG clade (including Metastelmatinae Endl. ex Meisn., Oxypetalinae K. Schum., and Gonolobinae (G. Don) Liede) (Liede & Täuber, 2000, 2002; Liede et al., 2002a, b; Rapini et al., 2003). More recently an additional subtribe, Orthosiinae Liede & Rapini, has been recognized within the MOG clade (Rapini et al., 2004; Liede-Schumann et al., 2005). Much progress has also been made in understanding relationships in the Old World tribe, Ceropegieae Decne. ex Orb. (Meve & Liede, 2001, 2002a, b), with its division into the four subtribes Anisotominae Meve & Liede, Leptadeniinae Meve & Liede, Heterostemminae Meve & Liede, and

Stapeliinae G. Don (Meve & Liede, 2004). An interactive key to the genera of Periplocoideae, Secamonoideae, and Asclepiadoideae, as presently delimited, has been made accessible on the Internet, together with descriptions of all genera and, as far as are available, illustrations (Liede-Schumann & Meve, 2006, <http://www.uni-bayreuth.de/departments/planta2/research/databases/delta_as/index.htm>).

In the more basal subfamilies Rauvolfioideae and Apocynoideae, in which the differences between genera are much greater than in the Asclepiadoideae, progress has been made mainly in improving tribal circumscriptions (Simões et al., 2004, 2006, for Mesechiteae; Endress et al., 2007, for Alyxieae and Vinceae).

Since the previous volume represented the Renaissance of the Apocynaceae, it seems only logical to think of this volume as the Enlightenment. Herein the fetters of traditional circumscriptions of taxa, especially at the generic, tribal, or subtribal level, are cast aside and new boundaries are delimited.

The symposium issue opens with a broad phylogenetic study of the Rauvolfioideae, the plesiomorphic, basalmost subfamily of the Apocynaceae. Its diverse array of flower and fruit types has made it difficult to ascertain generic and tribal relationships in the past (Endress et al., 2007). Simões et al. (2007) phylogenetically analyze 41 genera of Rauvolfioideae, including representatives from all nine tribes, using a combination of morphology and five regions of the chloroplast genome. The subfamily forms a paraphyletic grade to the rest of the family, with its taxa dispersed among 12 clades. Syncarpous ovaries, indehiscent fruits, winged seeds, and simple styleheads, all of which have played an important role in previous tribal delimitation, appear to have evolved in parallel numerous times. Thus, tribes in earlier classifications (Pichon, 1948, 1949, 1950b; Leeuwenberg, 1994) are almost all polyphyletic. Of the nine tribes of Rauvolfioideae recognized by Endress and Bruyns (2000), six were found to be monophyletic, whereas three were paraphyletic. Despite its paraphyly, Rauvolfioideae is maintained for the present. A revised classification is presented, in which the constituent genera are realigned into 10 tribes.

Next, by Alvarado-Cárdenas and Ochoterena (2007), is a morphological phylogenetic analysis of the *Cascabela*–*Thevetia* complex, utilizing 55 morphological characters, many employed here for the first time. The genera *Cascabela* Raf., *Cerbera* L., and *Thevetia* L. are similar morphologically, as is reflected by their convoluted taxonomic history, which also involves *Ahouai* Tourn. and *Plumeriopsis* Rusby & Woodson (Woodson, 1937; Gensel, 1969; Lippold, 1980; Williams, 1996). The detailed phylogenetic

analysis presented includes all currently recognized species of *Cascabela* and *Thevetia*, as well as at least one species of each genus of the Plumerieae, sensu Endress and Bruyns (2000). The results indicate that *Cascabela* and *Thevetia* form the crown clade of the Plumerieae. Because there are several easy-to-diagnose characters to distinguish between them, the authors argue for the recognition of both genera. Another important result of this paper is the insight it provides for the usefulness of less frequently used morphological characters.

Livshultz et al. (2007) present a phylogenetic analysis of the Apocynoideae, using four chloroplast DNA (cpDNA) regions and 16 morphological characters, in the most comprehensive analysis of the Apocynoideae to date, with representatives of 59 of the 77 genera now in the subfamily. Here, many of the polytomies or weakly supported branches of the tree in Potgieter and Albert (2001) are resolved with strong support, providing the long-awaited insight into relationships among genera. The Apocynoideae and tribes therein are non-monophyletic as delimited in Pichon (1950a), Leeuwenberg (1994), and Endress and Bruyns (2000) as amended by Simões et al. (2004). Instead, the authors find biogeography to be an accurate predictor of phylogeny. The non-monophyly of the traditional Asclepiadaceae and the sister group relationship of the three African genera of the Baisseeae (Pichon ex De Kruif) M. E. Endress (Apocynoideae; the new combination is made in Appendix 1) to Secamonoideae–Asclepiadoideae is strongly supported for the first time and corroborated by two other contributions to this volume (Simões et al., 2007; Lahaye et al., 2007). Pollen aggregation and mass transfer are reconstructed as having evolved in parallel multiple times within the Apocynoideae–Periplocoideae–Secamonoideae–Asclepiadoideae (APSA) clade, in agreement with the results of Ionta and Judd (2007) for Periplocoideae, presented in this issue. This major study of Apocynoideae is the complement to Simões et al. (2007) for Rauvolfioideae, which, together, treat all tribes of the Apocynaceae s. str.

The contribution of Ionta and Judd (2007) represents the first large-scale phylogenetic investigation of the Periplocoideae using ribosomal and plastid DNA. Periplocoideae are restricted to the Old World and are unique among the five subfamilies of Apocynaceae in that they include taxa with and without pollinia (Verhoeven & Venter, 2001). In this study, all but three of the 33 currently recognized genera of Periplocoideae were included. The affinities of many genera are illuminated, and the previous tribal circumscriptions of Venter and Verhoeven (1997) are not supported. The relationship of Periplocoideae to Apocynoideae and the Secamonoideae–Asclepia-

doideae clade, however, remains inconclusive. One of the most interesting results of this study is that pollinia in Periplocoideae are not only likely non-homologous with those in Secamonoideae–Asclepiadoideae, but that they have evolved at least three times in parallel within Periplocoideae.

Lahaye et al. (2007) present a molecular phylogeny of Madagascan Secamonoideae, which like Periplocoideae, are restricted to the Old World. The monophyly of *Pervillaea* Decne. and *Secamonopsis* Jum. is supported, whereas that of *Secamone* R. Br., by far the largest genus of the subfamily, is uncertain. The results suggest a recent and rapid diversification of Secamonoideae in Madagascar, with an explosive increase in morphological diversity. An unexpected bonus of the study is that the three African genera *Baissea* A. DC., *Motandra* A. DC., and *Oncinotis* Benth. of the Baisseeae are strongly supported as sister to the Secamonoideae–Asclepiadoideae clade, supporting results of Sennblad et al. (1998), Potgieter and Albert (2001), Livshultz et al. (2007), and Simões et al. (2007).

Meve and Liede-Schumann (2007) use chloroplast and nuclear DNA sequence data to investigate relationships within *Ceropegia* L., which, with 180 recognized species, is the largest genus of the Old World tribe Ceropegieae. The 36 analyzed species are dispersed in a grade composed of seven clades and are twice paraphyletic. The first paraphyly includes 11 species of *Ceropegia* together with all eight *Brachystelma* Sims exemplars. For the second paraphyly, the six endemic Madagascan *Ceropegia* species investigated and the East African species *C. robynsiana* Werderm. form an unresolved clade together with the 10 included stapeliads. Because no morphological, anatomical, or karyological characters are known at present to differentiate between these genera, the authors argue for a continued recognition of a paraphyletic *Ceropegia* for the time being.

Rapini et al. (2007) provide a biogeographic study of the New World Asclepiadoideae employing Bayesian inference and molecular dating on data from floristic inventories and 216 cpDNA sequences. In this analysis, the Asclepiadoideae are reconstructed as having arisen somewhere in the Old World 40 million years ago (Ma), confirming earlier hypotheses of an African origin for the subfamily (Macfarlane, 1933; Good, 1956; Meve & Liede, 2002b), fitting nicely with the sister relationship between the Secamonoideae–Asclepiadoideae clade and the African Baisseinae (Apocynoideae) reported here by Lahaye et al. (2007) and Livshultz et al. (2007). Four independent dispersal events to the New World are hypothesized: (1) the MOG clade (Metastelmatinae, Oxypetalinae, and Gonolobinae) colonized South

America via transoceanic long-distance dispersal from Africa 32 Ma; (2) *Cynanchum* L. subg. *Mellichampia* (A. Gray) Woodson (Cynanchinae) arrived in the New World 24 Ma; (3) *Asclepias* L. (Asclepiadinae) reached North America via the Bering Strait 20 Ma; and (4) *Marsdenia* R. Br. probably arrived in the New World 16 Ma.

In closer focus, Goyder et al. (2007) use nuclear and cpDNA to infer phylogenetic relationships among 19 of the 24 currently recognized genera in subtribe Asclepiadinae, particularly among the predominantly non-twining herbaceous genera around *Asclepias*. The subtribe is strongly supported as monophyletic, but generic delimitations, which have long been a source of contention (e.g., Brown, 1902–1903; Bullock, 1952; Goyder, 1995, 1998, 2001a, b), need to be revised. Either *Asclepias* should be expanded to encompass the entire subtribe, or it should be restricted to the New World and the generic limits of the Old World members should be redefined. The traditional floral characters that have been used to differentiate genera were found to be unreliable due to parallelism; vegetative features could prove to be more useful in this subtribe.

Oxypetalum R. Br. is one of the most characteristic and species-rich genera of Asclepiadoideae in southeastern Brazil. It is difficult to go into the field in this region without seeing at least one species of this genus. *Oxypetalum* belongs to the tribe Asclepiadeae, where recent phylogenetic studies place it in the Oxypetalinae core group (Liede-Schumann et al., 2005), the crown clade of the large and diverse MOC clade (Rapini et al., 2003, 2006). Marquete et al. (2007) revise the genus in Rio de Janeiro State, Brazil. Twenty-one species are recognized, of which four are endemic. A key to the species is included, and eight species are beautifully illustrated.

The ability of ithomiine and danaïne butterflies to sequester pyrrolizidine alkaloids (PAs) and to use them for their own benefit is a well-known and fascinating phenomenon (e.g., Boppré, 1986). Here, Brehm et al. (2007) report the presence of PAs, including two novel retronecine monoesters, for the first time in *Prestonia amabilis* J. F. Morales (Apocynoideae, Echiteae) and their uptake by adults of eight species belonging to two groups of Lepidoptera: Ithomiinae butterflies (Nymphalidae) and Arctiinae moths (Arctiidae). It is postulated that *Prestonia* ancestors may have served as an ancestral source of PAs in the evolution of pharmacophagous behavior in the Ithomiinae butterflies. The presence of PAs has been documented for some species of *Parsonsia* R. Br., also in Echiteae (Edgar, 1984; Trigo et al., 1996). Another paper in this volume (Livshultz et al., 2007) documents phylogenetically for the first time the sister

relationship of *Parsonsia* and *Prestonia*, despite the fact that the former genus is restricted to Asia and Australia and the latter to the Neotropics.

Postzygotic self-incompatibility has been demonstrated in some species of the evolutionarily advanced taxa of the APSA clade (Wyatt et al., 1998; Lipow & Wyatt, 1999, 2000), in which mixed loads of self- and cross-pollen could cause abortion of whole fruits and thus extreme waste of both cross-pollen and cross-fertilized ovules. Here, Wyatt and Lipow (2007) hypothesize that the evolution of pollinia and loss of a compitum in Apocynaceae s.l. are adaptations to prevent or compensate for the wasteful effects of mixed pollen loads. Having pollen massed together into pollinia provides that all of the pollen delivered to the stigmatic chambers during a single pollination event will be either compatible or incompatible. A compatible pollination will result in follicles with a full complement of cross-pollinated seeds (Broyles & Wyatt, 1990). Loss of the compitum enables one carpel to produce a follicle, even if the other one aborts from a mixed load of pollen.

More et al. (2007) report on the pollination biology of three night-flowering species of *Mandevilla* Lindl. native to Argentina, which are pollinated exclusively by long-tongued hawkmoths. They found that the two species with the longest corolla tubes (*M. longiflora* (Desf.) Pichon and *M. petraea* (A. St.-Hil.) Pichon, both with corolla tubes greater than 10 cm long) are pollinated by long- to very-long-tongued hawkmoths. Thus in these two species, the pollinator spectrum is restricted by the extremely long and slender corolla tube, a common strategy in various plant families (Grant & Grant, 1983a, b; Nilsson, 1988; Endress, 1994; Proctor et al., 1996; Johnson & Steiner, 1997). Surprisingly, the third species of *Mandevilla* investigated, *M. laxa* (Ruiz & Pav.) Woodson, with much shorter corolla tubes about 4 cm long, was also found to be pollinated by species of long- to very-long-tongued hawkmoths, with proboscis lengths greatly exceeding that of the corolla tube. In this species, the limiting factor was not the length of the corolla tube, but the operative width of the pollination chambers, which were too narrow for short-tongued hawkmoths, which have wider proboscides. Thus, in *Mandevilla*, both corolla tube length and operative width play an important role in restricting access to the flowers.

Finally, because floral morphology may also influence pollinator behavior and pollen transfer among New World *Asclepias*, Theiss et al. (2007) use multiple measures to evaluate the efficiency and effectiveness of diverse generalist pollinators on three sympatric species: *A. syriaca* L., *A. incarnata* L., and *A. verticillata* L. Except for the fidelity of butterflies on *A. incarnata* and the prevalence and constancy of

honeybees on *A. syriaca*, native North American bumblebees, carpenter bees, and sphecids wasps rank highest in all measures of pollinator effectiveness and exhibit less potential for geitonogamous pollen transfer than introduced honeybees. Pollinator effectiveness also varies with plant species, as insects carry more pollinia of *A. incarnata* and *A. verticillata* than of *A. syriaca* but appear more likely to insert *A. syriaca* pollinia into subsequent flowers, based on vector pollen loads from 15 sites. Even so, the high variability and individualistic actions of pollinators highlight the need for further study of spatio-temporal variation in pollinator effectiveness.

Although we have made great strides in our understanding of the phylogeny and relationships of the Apocynaceae in recent years, there remain certain regions of the family that are still poorly known, and even in those regions that are better investigated, there are taxonomic gaps to fill. It has become increasingly clear that both Rauvolfioideae and Apocynoideae are paraphyletic. We need to address this and find the most feasible resolution. Within the Rauvolfioideae, we particularly need to rigorously study Willughbeieae to determine generic limits and intertribal relationships. In Vinceae, we still lack conclusive evidence as to whether *Neisosperma* Raf. should be maintained as a genus distinct from *Ochrosia* Juss., and the systematic position of *Amsonia* Walter, which has been excluded from Vinceae (Endress et al., 2007), remains uncertain. We need to confirm the taxonomic composition of Melodineae and sort out its relationship with Hunterieae. In Apocynoideae, the relatives of *Rhabdadenia* Müll. Arg. and *Galactophora* Woodson need to be better investigated. Generic limits in Echiteae cry out to be elucidated; presently some genera are more or less defined only by the absence of a single morphological characteristic (e.g., *Laubertia* A. DC. is distinguished from closely related genera by the lack of calycine colleters). This is unsatisfactory, and we need to study the relationships within this tribe in greater depth and to search out new morphological characters to convincingly circumscribe its component genera. Despite the ever-increasing number of genetic regions analyzed and a significant new phylogeny of the Periplocoideae, their placement within the APSA clade remains uncertain. Certain floral specializations in the Periplocoideae, such as the staminal feet (Endress & Bruyns, 2000) and translators, appear to be morphologically intermediate between Apocynoideae and Secamonoideae–Asclepiadoideae. Until the systematic position of the Periplocoideae is elucidated, however, any hypotheses as to their evolutionary position are without substance. In Secamonoideae, most of the species molecularly studied to date are

Madagascan; we need to strive for a broader sampling. The relationship of the mainly Asian *Toxocarpus* Wight & Arn. to *Secamone* is undetermined, and solving this conundrum would be a logical target in this subfamily. In Asclepiadoideae, the Marsdenieae is the tribe most in need of careful study. The first steps have been made in delimiting the large genus *Hoya* R. Br. from other genera in the *Hoya* alliance (Wanntorp et al., 2006; Wanntorp & Forster, 2007). Similarly, it remains to be determined whether the many satellite genera split off from *Marsdenia* deserve taxonomic recognition. The systematic position of the two enigmatic genera *Eustegia* R. Br. and *Emicarpus* K. Schum. & Schltr. within Asclepiadoideae remains unclear. In Asclepiadeae, the larger genera of the MOC clade in South America are still insufficiently delimited, and their species numbers are uncertain.

Appendix 1 is an updated classification scheme for the Apocynaceae s.l. that lists subfamilies, tribes, and subtribes, incorporating the results presented in this symposium issue. The additional tribes and subtribes not present in the outline presented by Endress and Stevens (2001) are preceded by an asterisk.

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- APPENDIX 1. Revised classification scheme for the Apocynaceae. The additional tribes and subtribes not present in the outline presented by Endress and Stevens (2001) are preceded by an asterisk.
- RAUVOLFIOIDEAE** Kostel. TYPE: *Rauwolfia* L. (83 genera)
- ***Aspidospermeae** Miers. TYPE: *Aspidosperma* Mart. & Zucc. (6 genera)
- Aspidosperma* Mart. & Zucc., *Geissospermum* Allemão, *Haplophyton* A. DC., *Microplumeria* Baill., *Strempeliopsis* Benth., *Vallesia* Ruiz & Pav.
- Alstonieae** G. Don. TYPE: *Alstonia* R. Br. (2 genera)
- Alstonia* R. Br., *Dyera* Hook. f.
- Vinceae** Duby. TYPE: *Vinca* L. (9 genera)
- Catharanthus* G. Don, *Kamettia* Kostel., *Kopsia* Blume, *Laxoplumeria* Markgr., *Ochrosia* Juss., *Petchia* Livera, *Rauwolfia* L., *Tonduzia* Pittier, *Vinca* L.
- Willughbeieae** A. DC. TYPE: *Willughbeia* Roxb. (18 genera)
- Ancylobotrys* Pierre, *Bousigonia* Pierre, *Chamaeclitandra* (Stapf) Pichon, *Clitandra* Benth., *Couma* Aubl., *Cyclocotyla* Stapf, *Cylindropsis* Pierre, *Dictyophleba* Pierre, *Hancornia* Gomes, *Lacmellea* H. Karst., *Landolphia* P. Beauv., *Leuconotis* Jack, *Orthopichonia* H. Huber, *Paracouria* Aubl., *Parahancornia* Ducke, *Saba* (Pichon) Pichon, *Vahadenia* Stapf, *Willughbeia* Roxb.
- Tabernaemontaneae** G. Don. TYPE: *Tabernaemontana* L. (19 genera)
- Ambelania* Aubl., *Bonafousia* A. DC., *Callichilia* Stapf, *Calocrater* K. Schum., *Carvalhoa* K. Schum., *Crioceras* Pierre, *Macoubea* Aubl., *Molongum* Pichon, *Mucoa* Zarucchi, *Neocouma* Pierre, *Rhigospira* Miers, *Schizozygia* Baill., *Spongiosperma* Zarucchi, *Stemmadenia* Benth., *Stenosolen* (Müll. Arg.) Markgr., *Tabernaemontana* L., *Tabernanthe* Baill., *Voacanga* Thouars, *Woytkowskia* Woodson
- Melodineae** G. Don. TYPE: *Melodinus* J. R. Forst. & G. Forst. (4 genera)
- Craspidospermum* Bojer ex A. DC., *Melodinus* J. R. Forst. & G. Forst., *Pycnobotrya* Benth., *Stephanostegia* Baill.
- Alyxieae** G. Don. TYPE: *Alyxia* Banks ex R. Br. (7 genera)
- Alyxia* Banks ex R. Br., *Chilocarpus* Blume, *Condylocarpon* Desf., *Lepinia* Decne., *Lepiniopsis* Valetton, *Plectaneia* Thouars, *Pteralyxia* K. Schum.
- Hunterieae** Miers. TYPE: *Hunteria* Roxb. (4 genera)
- Gonioma* E. Mey., *Hunteria* Roxb., *Picralima* Pierre, *Pleiocarpa* Benth.
- Plumerieae** E. Mey. TYPE: *Plumeria* L. (10 genera)
- Allamanda* L., *Anechites* Griseb., *Cameraria* L., *Cerbera* L., *Cerberiopsis* Vieill. ex Pancher & Sébert, *Himatanthus* Willd. ex Schult., *Mortoniella* Woodson, *Plumeria* L., *Skytanthus* Meyen, *Thevetia* L.
- Carisseae** Dumort. TYPE: *Carissa* L. (2 genera)
- Acokanthera* G. Don, *Carissa* L.
- Rauvolfioideae incertae sedis** (2 genera)
- Amsonia* Walter, *Diplorhynchus* Welw. ex Ficalho & Hiern.

APOCYNOIDAE Burnett. TYPE: *Apocynum* L. (80 genera)

Wrightieae G. Don. TYPE: *Wrightia* R. Br. (3 genera)
Pleioceras Baill., *Stephanostema* K. Schum.,
Wrightia R. Br.

***Nerieae** Baill. TYPE: *Nerium* L. (6 genera)
Adenium Roem. & Schult., *Alafia* Thouars,
Farquharia Stapf, *Isonema* R. Br., *Nerium* L.,
Strophanthus DC.

Malouetiae Müll. Arg. TYPE: *Malouetia* A. DC. (11 genera)

Allowoodsonia Markgr., *Carruthersia* Seem.,
Funtumia Stapf, *Holarrhena* R. Br., *Kibatalia*
G. Don, *Malouetia* A. DC., *Malouetiella* Pichon,
Mascarenhasia A. DC., *Neobraccia* Britton, *Pachypodium* Lindl., *Spirolobium* Baill.

Apocynae Rehb. TYPE: *Apocynum* L. (23 genera)

Aganonerion Pierre ex Spire, *Aganosma* (Blume)
G. Don, *Amalocalyx* Pierre, *Amphineurion* (A.
DC.) Pichon, *Anodendron* A. DC., *Apocynum* L.,
Baharuia D. J. Middleton, *Beaumontia* Wall.,
Chonemorpha G. Don, *Cleghornia* Wight, *Dewevrella* De Wild., *Epigynum* Wight, *Ichnocarpus*
R. Br., *Ixodonerium* Pit., *Micrechites* Miq.,
Papuechites Markgr., *Parameria* Benth., *Parepi-
gynum* Tsiang & P. T. Li, *Pottsia* Hook. & Arn.,
Sindechites Oliv., *Trachelospermum* Lem., *Ur-
ceola* Roxb., *Vallaris* Burm. f.

***Odontadeniae** Miers. TYPE: *Odontadenia* Benth. (6 genera)

Cycladenia Benth., *Elytropus* Müll. Arg., *Odon-
tadenia* Benth., *Secondatia* A. DC., *Stipecoma*
Müll. Arg., *Thyrsanthella* (Baill.) Pichon

Mesechiteae Miers. TYPE: *Mesechites* Müll. Arg. (5 genera)

Allomarkgrafia Woodson, *Forsteronia* G. Mey.,
Mandevilla Lindl., *Mesechites* Müll. Arg., *Tintin-
nabularia* Woodson

Echiteae G. Don. TYPE: *Echites* P. Browne (20 genera)

Ingadenia Miers, *Artia* Guillaumin, *Asketanthera*
Woodson, *Bahiella* J. F. Morales, *Echites* P.
Browne, *Ecua* D. J. Middleton, *Fernaldia*
Woodson, *Hylaea* J. F. Morales, *Laubertia* A.
DC., *Macropharynx* Rusby, *Parsonsia* R. Br.,
Peltastes Woodson, *Pentalinon* Voigt, *Prestonia*
R. Br., *Rhabdadenia* Müll. Arg., *Rhodocalyx*
Müll. Arg., *Salpinctes* Woodson, *Temnadenia*
Miers, *Thenardia* Kunth, *Thoreauca* J. K.
Williams

***Baisseeae** (Pichon ex De Kruif) M. E. Endress, stat.
nov. Baisseinae Pichon ex De Kruif, Meded.
Landbouwhoogeschool Wageningen 83(7): 2. 1983.
TYPE: *Baissea* A. DC. 1844 (3 genera)

Baissea A. DC., *Motandra* A. DC., *Oncinotis*
Benth.

Apocynoideae incertae sedis (3 genera)

Eucorymbia Stapf, *Galactophora* Woodson, *Val-
lariopsis* Woodson

PERIPLOCOIDEAE R. Br. ex Endl. TYPE: *Periploca* L. (33 genera)

Atherandra Decne., *Baroniella* Costantin &
Gallaud, *Baseonema* Schltr. & Rendle, *Bate-
santhus* N. E. Br., *Buckollia* Venter & R. L.
Verh., *Camptocarpus* Decne., *Cryptolepis* R. Br.,
Cryptostegia R. Br., *Decalepis* Wight & Arn.,
Ectadium E. Mey., *Epistemma* D. V. Field & J.

B. Hall, *Finlaysonia* Wall., *Gymnanthera* R. Br.,
Hemidesmus R. Br., *Kappia* Venter, A. P. Dold &
R. L. Verh., *Ischnolepis* Jum. & H. Perrier,
Maclaudia Venter & R. L. Verh., *Mondia* Skeels,
Myriopteron Griff., *Omphalogonus* Baill., *Pento-
petia* Decne., *Periploca* L., *Petopentia* Bullock,
Phyllanthera Blume, *Raphionacme* Harv., *Sa-
cleuxia* Baill., *Sarcorrhiza* Bullock, *Schlechterella*
K. Schum., *Stomatostemma* N. E. Br., *Strepto-
caulon* Wight & Arn., *Tacazzea* Decne., *Tele-
ctadium* Baill., *Zygostelma* Benth.

SECAMONOIDEAE Endl. (8 genera)

Secamoneae G. Don. TYPE: *Secamone* R. Br.

Calyptranthera Klack., *Genianthus* Hook. f.,
Goniostemma Wight, *Perrillaea* Decne., *Seca-
mone* R. Br., *Secamonopsis* Jum., *Toxocarpus*
Wight & Arn., *Trichosandra* Decne.

ASCLEPIADOIDEAE R. Br. ex Burnett. TYPE: *Asclepias*
L. (172 genera)

Fockeeae Kunze, Meve & Liede. TYPE: *Fockea* Endl. (2 genera)

Cibirhiza Bruyns, *Fockea* Endl.

Marsdeniae Benth. TYPE: *Marsdenia* R. Br. (27 genera)

Anatropanthus Schltr., *Anisopus* N. E. Br.,
Asterostemma Decne., *Campestigma* Pierre ex
Costantin, *Cathetostemma* Blume, *Cionura* Gri-
seb., *Clemensiella* Schltr., *Cosmostigma* Wight,
Dischidia R. Br., *Dolichopetalum* Tsiang, *Gon-
gronema* (Endl.) Decne., *Gunnessia* P. I. Forst.,
Gymnema R. Br., *Heynella* Backer, *Hoya* R. Br.,
Jasminanthes Blume, *Lygisma* Hook. f., *Marsde-
nia* R. Br., *Oreosparte* Schltr., *Pycnorhachis*
Benth., *Rhyssolobium* E. Mey., *Sarcolobus* R.
Br., *Stephanotis* Thouars, *Stigmatorhynchus*
Schltr., *Telosma* Coville, *Treutlera* Hook. f.,
Wattakaka Hassk.

Ceropegiae Decne. ex Orb. TYPE: *Ceropegia* L. (46 genera)

***Anisotominae** Meve & Liede. TYPE: *Anisotoma*
Fenzl (5 genera)

Anisotoma Fenzl, *Emplectanthus* N. E. Br.,
Neoschumannia Schltr., *Riocreuxia* Decne.,
Sisyranthus E. Mey.

***Heterostemminae** Meve & Liede. TYPE: *Hetero-
stemma* Wight & Arn. (1 genus)

Heterostemma Wight & Arn.

***Leptadeniinae** Meve & Liede. TYPE: *Leptadenia*
R. Br. (4 genera)

Conomitra Fenzl, *Leptadenia* R. Br.,
Orthanthera Wight, *Pentasachme* Wall. ex
Wight

***Stapeliinae** G. Don. TYPE: *Stapelia* L. (35 genera)

Apteranthes J. C. Mikan, *Australluma* Plowes,
Baynesia Bruyns, *Boucerosia* Wight & Arn.,
Brachystelma Sims, *Caralluma* R. Br., *Cau-
danthera* Plowes, *Ceropegia* L., *Desmidorchis*
Ehrenb., *Duralia* Haw., *Duraliandra* M. G.
Gilbert, *Echidnopsis* Hook. f., *Edithecolea* N.
E. Br., *Hoodia* Sweet ex Decne., *Huernia* R.
Br., *Larryleachia* Plowes, *Larrania* Plowes,
Monolluma Plowes, *Notechidnopsis* Lavranos
& Bleck, *Ophionella* Bruyns, *Orbea* Haw.,
Orbeanthus L. C. Leach, *Pectinaria* Haw.,
Piarranthus R. Br., *Pseudolithos* P. R. O.
Bally, *Quaqua* N. E. Br., *Rhytidocaulon* P. R.

O. Bally, *Richtersveldia* Meve & Liede, *Socotrella* Bruyns & A. G. Miller, *Stapelia* L., *Stapelianthus* Choux ex A. C. White & B. Sloane, *Stapeliopsis* Pillans, *Tavaresia* Welw., *Tridentea* Haw., *Tromotriche* Haw., *White-Sloanea* Chiov.

Asclepiadeae (R. Br.) Duby. TYPE: *Asclepias* L. (97 genera)

***Astephaninae** Endl. ex Meisn. TYPE: *Astephanus* R. Br. (3 genera)

Astephanus R. Br., *Microloma* R. Br., *Oncinema* Arn.

***Asclepiadinae** Endl. ex Meisn. TYPE: *Asclepias* L. (23 genera)

Aidomene Stopp, *Asclepias* L., *Aspidoglossum* E. Mey., *Aspidonepsis* Nicholas & Goyder, *Calotropis* R. Br., *Cordylogyne* E. Mey., *Fanninia* Harv., *Glossostelma* Schltr., *Gomphocarpus* R. Br., *Kanahia* R. Br., *Lagarinthus* E. Mey., *Margaretta* Oliv., *Miraglossum* Kupicha, *Odontostelma* Rendle, *Pachycarpus* E. Mey., *Parapodium* E. Mey., *Pergularia* L., *Schizoglossum* E. Mey., *Stathmostelma* K. Schum., *Stenostelma* Schltr., *Trachycalymma* Bullock, *Woodia* Schltr., *Xysmalobium* R. Br.

***Tylophorinae** (K. Schum.) Liede. TYPE: *Tylophora* R. Br. (9 genera)

Biondia Schltr., *Blyttia* Arn., *Diplostigma* K. Schum., *Goydera* Liede, *Pentatropis* R. Br., *Pleurostelma* Baill., *Rhyncharrhena* F. Muell., *Tylophora* R. Br., *Vincetoxicum* Wolf

***Cynanchinae** K. Schum. TYPE: *Cynanchum* L. (14 genera)

Adelostemma Hook. f., *Cynanchum* L., *Glossonema* Decne., *Graphistemma* (Champ. ex Benth.) Champ. ex Benth., *Holostemma* R. Br., *Mahawoa* Schltr., *Merrillanthus* Chun & Tsiang, *Metaplexis* R. Br., *Odontanthera*

Wight, *Pentarrhinum* E. Mey., *Pentastelma* Tsiang & P. T. Li, *Raphistemma* Wall., *Schizostephanus* Hochst. ex Benth., *Sichuania* M. G. Gilbert & P. T. Li

***Metastelmatinae** Endl. ex Meisn. TYPE: *Metastelma* R. Br. (14 genera)

Barjonia Decne., *Blepharodon* Decne., *Ditassa* R. Br., *Hemipogon* Decne., *Hypolobus* E. Fourn., *Macroditassa* Malme, *Metastelma* R. Br., *Minaria* T. U. P. Konno & Rapini, *Nautonia* Decne., *Nephradenia* Decne., *Peplonia* Decne., *Petalostelma* E. Fourn., *Rhysostelma* Decne., *Tassadia* Decne.

***Orthosiinae** Liede & Rapini. TYPE: *Orthosia* Decne. (3 genera)

Jobinia E. Fourn., *Orthosia* Decne., *Scyphostelma* Baill.

***Oxypetalinae** K. Schum. TYPE: *Oxypetalum* R. Br. (10 genera)

Amblyopetalum (Griseb.) Malme, *Araujia* Brot., *Funastrum* E. Fourn., *Morrenia* Lindl., *Oxypetalum* R. Br., *Philibertia* Kunth, *Schistogyne* Hook. & Arn., *Stenomeria* Turcz., *Tweedia* Hook. & Arn., *Widgrenia* Malme

***Gonolobinae** (G. Don) Liede. TYPE: *Gonolobus* Michx. (13 genera)

Dictyanthus Decne., *Fischeria* DC., *Gonolobus* Michx., *Gyrostelma* E. Fourn., *Macroscepis* Kunth, *Matelea* Aubl., *Pherotrichis* Decne., *Polystemma* Decne., *Prosthecidiscus* Donn. Sm., *Rojasia* Malme, *Schubertia* Mart., *Stelma* Baill., *Trichosacme* Zucc.

Asclepiadeae incertae sedis (8 genera)

Calciophila Liede & Meve, *Diplolepis* R. Br., *Emicocarpus* K. Schum. & Schltr., *Eustegia* R. Br., *Oxystelma* R. Br., *Pentacyphus* Schltr., *Seshagiria* Ansari & Hemadri, *Solenostemma* Hayne